The impact of recent increases in atmospheric CO₂ on biomass production and vegetative retention of Cheatgrass (*Bromus tectorum*): implications for fire disturbance

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Abstract

Cheatgrass (Bromus tectorum) is a recognized, invasive annual weed of the western United States that reduces fire return times from decades to less than 5 years. To determine the interaction between rising carbon dioxide concentration ([CO₂]) and fuel load, we characterized potential changes in biomass accumulation, C:N ratio and digestibility of three cheatgrass populations from different elevations to recent and nearterm projections in atmospheric [CO₂]. The experimental CO₂ values (270, 320, 370, 420 µmol mol⁻¹) corresponded roughly to the CO₂ concentrations that existed at the beginning of the 19th century, that during the 1960s, the current [CO₂], and the near-term [CO₂] projection for 2020, respectively. From 25 until 87 days after sowing (DAS), aboveground biomass for these different populations increased 1.5-2.7 g per plant for every 10 μmol mol⁻¹ increase above the 270 μmol mol⁻¹ preindustrial baseline. CO₂ sensitivity among populations varied with elevational origin with populations from the lowest elevation showing the greatest productivity. Among all populations, the undigestible portion of aboveground plant material (acid detergent fiber ADF, mostly cellulose and lignin) increased with increasing [CO₂]. In addition, the ratio of C:N increased with leaf age, with [CO₂] and was highest for the lower elevational population. These CO₂-induced qualitative changes could, in turn, result in potential decreases in herbivory and decomposition with subsequent effects on the aboveground retention of cheatgrass biomass. Overall, these data suggest that increasing atmospheric [CO₂] above preambient levels may have contributed significantly to cheatgrass productivity and fuel load with subsequent effects on fire frequency and intensity.

Keywords: Carbon dioxide, cheatgrass, fire frequency, invasive weeds

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Introduction

Invasive plants are generally recognized as those species, usually non-native for a given system, whose introduction, commonly by human transport, results in appreciable economic or environmental damage (Mooney & Hobbs, 2000). One instance of environmental damage related to invasive species success is alteration of the fire cycle within plant communities. Such cycles are accelerated by the invasion of rapidly

Correspondence: L. H. Ziska, e-mail: lziska@asrr.arsusda.gov Tel: 301-504-6639, fax: 301-504-5823 growing, fire-tolerant species (usually grasses) that produce combustive vegetation with subsequent increases in the frequency and spread of natural or anthropogenic fires (D'Antonio & Vitousek, 1992).

For the western United States, cheatgrass (*Bromus tectorum*), originally introduced from central Asia, has spread rapidly throughout the intermountain west as a result of livestock movement and overgrazing (Mack, 1986). Growing quickly in mesic and xerophytic environments, cheatgrass can colonize open spaces between perennial, native shrubs with a fine, flammable material that increases the frequency of fire events (Billings, 1990, 1994). Because cheatgrass is fire-adapted, increas-

ing fire frequency favors its establishment and spread. The conversion of the shrub-dominated steppes of the western US to a cheatgrass dominated landscape during the 20th century remains one of the quintessential examples of how invasive-induced increases in the fire cycle can significantly alter plant communities (see Fig. 1 in Sage, 1996).

Since the late-1950s, records of carbon dioxide concentration ([CO2]) obtained from the Mauna Loa observatory in Hawaii have shown an increase in [CO₂] of about 20% from 311 to 375 µmol mol⁻¹ (Keeling & Whorf, 2001). The current annual rate of [CO₂] increase ($\sim 0.5\%$) is expected to continue with concentrations exceeding $600 \,\mu\text{mol mol}^{-1}$ by the end of the 21st century (Schimel et al., 1996). Because current atmospheric [CO₂] is less than optimal for photosynthesis, as atmospheric [CO₂] increases, plant growth may be stimulated, depending on species. Increasing [CO2] in turn, could contribute to the overall growth of an invasive, fire-tolerant species. These CO₂-induced changes in vegetation would have subsequent effects on time needed to reach a minimum fuel threshold and the total fuel load. In addition, rising [CO₂] could also affect qualitative aspects of vegetation that could alter aboveground persistence (e.g. decomposition) with subsequent effects on fuel load. However, in general, the impact of rising [CO₂] on fire disturbance regimes has not been well studied (see Sage, 1996 for a review).

A limited number of experiments have indicated that doubling atmospheric carbon dioxide ($\sim 680\,\mu\mathrm{mol}\,\mathrm{mol}^{-1}$) to simulate future abiotic conditions significantly increases cheatgrass biomass (1.39–1.93 × ambient), suggesting that its productivity could be particularly responsive to future [CO₂] (Smith *et al.*, 1987; Poorter, 1993). However, the photosynthetic response to [CO₂] is not linear; consequently, it is difficult to extrapolate the sensitivity of cheatgrass growth to recent [CO₂] increases or near-term [CO₂] projections based only on 2 × ambient observations. Moreover, [CO₂] responsiveness, *per se*, does not address qualitative changes in potential digestibility or decomposition, which would also contribute to standing fuel load.

To systematically address the relative extent of potential growth stimulation and qualitative parameters over a range of [CO₂]s that have already occurred, or will occur in the near term (i.e. <20 years), we grew three different populations of cheatgrass collected in the Sierra Nevada Mountains at 270, 320, 370 or 420 μ mol mol⁻¹ [CO₂] for a 3-month period. The CO₂ values used correspond approximately to those that existed at the beginning of the 19th century, that during the 1960s, the current [CO₂], and the nearterm [CO₂] projection for 2020, respectively. Our overall objective was to ascertain the impact of rising [CO₂] on

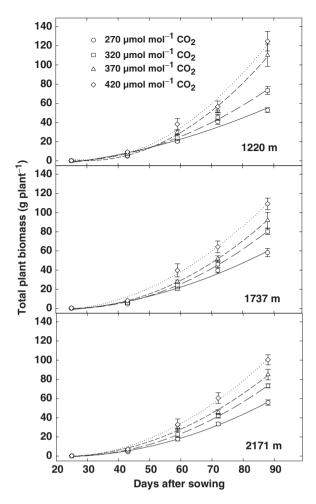


Fig. 1 Total biomass of cheatgrass (*Bromus tectorum* g per plant) over time (days after sowing, DAS) as a function of increasing $[CO_2]$ for three populations collected at different elevations in northern Nevada. Significant $[CO_2]$ differences were observed after 59 DAS. Bars are \pm SE.

potential changes in fire ecology by quantifying changes in growth, final standing biomass, digestibility and the C:N ratio of cheatgrass populations.

Materials and methods

Experimental conditions. Cheatgrass (B. tectorum) seed was collected at low, mid and high elevations in Northern Nevada. The low elevation collection site (1220 m) was north of Rye Patch Reservoir (40.28°N, 118.19°W). This shadscale (Atriplex confertifolia) community receives on average 18 cm of yearly precipitation and burned in 1999. The mid-elevation site (1737) was at Emigrant Pass (40.38°N, 116.18°W) and is a Wyoming big sagebrush (Artemisa tridentata subspecies wyomingensis) dominated community that

receives a yearly average of 30 cm of precipitation. The high elevation site (2171 m) is near the summit of Fox Mountain (41.00°N, 119.33°W) and is dominated by bluebunch wheatgrass (Pseudoroegneria spicata) and receives about 45 cm of yearly precipitation. Collected seed was pretreated at 5 °C until germination (testa was visible), then planted. Two to three seeds were sown in pots filled with a 1:1 mixture of sand and vermiculite and thinned to one seedling 4-6 days after emergence. For each CO₂ treatment and population, 30-35 pots were used. To avoid root binding and because of space considerations, different pot volumes, from 0.6 to 22.1 L were used, with the smaller pots being sampled first. The height of all pots was made uniform to avoid differences in light (photosynthetically active radiation (PAR)) intensity. For each CO₂ treatment, pots were watered to the drip point daily with a complete nutrient solution containing 14.5 mmol m⁻³ nitrogen (Robinson, 1984).

Because no experimental system has yet been devised to expose plants to subambient [CO2] under field conditions for 24 h day⁻¹ (see Mayeux et al., 1993), the study was conducted using controlled environment chambers (EGC Corporation., Chagrin Falls, OH, USA) at Beltsville, MD with a given chamber set at one of four $[CO_2]$ setpoints (270, 320, 370 and 420 μ mol mol⁻¹) for 24 h day⁻¹. The concentrations used approximated atmospheric [CO₂] at the beginning of the 19th century, that during the 1960s, current ambient, and that projected by the year 2020. Actual average 24 h [CO₂] values (\pm SD) were 283 \pm 16, 323 \pm 12, 372 \pm 9 $425 \pm 14 \,\mu\text{mol mol}^{-1}$. For all temperature was altered in a diurnal fashion (in steps) from an overnight low of 15 °C to a maximum afternoon value of 25 °C, with an average daily (24 h) value of 18.3 °C. Similarly, PAR was also altered concurrently with temperature, with the highest PAR value $(900-1000 \, \mu \text{mol m}^2 \, \text{s}^{-1})$ occurring during the afternoon (12:00-15:00 hours). Daily PAR was 14 h, supplied by a mixture of high-pressure sodium and metal halide lamps. The [CO₂] of the air within each chamber was controlled by adding either CO₂ or CO₂ free air to maintain the set concentration. Injection of CO₂ and CO₂-free air was controlled by a TC-2 controller using input from an absolute infrared gas analyzer (WMA-2, PP Systems, Haverhill, MA, USA). Typical examples of a diurnal temperature/PAR curve for these experimental chambers can be found in Ziska et al. (2001).

Vegetative measurements. Plants were grown until 87 days after sowing (DAS), by which time floral spikes had matured for the lowest elevational population (bolting did not occur for the other two populations). A

[CO₂] increase of 150 umol mol⁻¹ decreased floral times for this elevational population by approximately 10 days. Destructive harvest of five to six plants for each [CO₂] and population occurred at 25, 43, 59, 72 and 87 DAS. Root weights for the initial harvest avearaged less than 0.2 g, with no indication of root binding. Because larger pots were used with successive harvests, root binding did not occur during the experiment. For the first three harvests, leaf area was determined photometrically using a leaf area meter (Model 3100, Li-Cor Corporation, Lincoln, NE, USA). Given the large leaf area at 72 and 87 DAS, subsamples of 15-20 leaves per population and [CO₂] were placed in moistened paper towels to prevent desiccation and leaf area determined as described above. Leaf subsamples were then dried at 65 °C and total leaf area per plant and specific leaf weight estimated by the linear regression of leaf area to leaf dry weight ($r^2 > 0.91$ for all treatments). In addition to leaf area, dry mass was determined separately for all leaves, stems, roots and floral spikes (if present) for each harvest for all treatments following drying at 65 °C for a minimum of 48 h or until dry mass was constant.

Carbon and nitrogen analysis. Carbon was quantified by a modified Walkley-Black procedure (Walkley, 1947) using supplemental heating to 180 °C with a Bunsen burner. No correction factor was used. Tissue N was digested using a microKjeldahl method (Isaac & Johnson, 1976). Ammonium in the digest was quantified using a total Kjeldahl module for the Lachat flow injection system. An apple leaf plant tissue standard (NIST 1515) was used to check method accuracy for total N and C. Determinations of shoot carbon and nitrogen were made for individual plants for all populations and [CO₂] treatments at 43, 59, 74 and 87 DAS.

Digestibility. Samples were obtained for the last three sampling dates (59, 74 and 87 DAS) for all treatments. All samples were analyzed as single reps for neutral detergent fiber (NDF, basically, hemicellulose, cellulose and lignin), acid detergent fiber (ADF, nondigestible lignin and cellulose), and 72% sulfuric acid lignin (ADL) (Goering & Van Soest, 1970; Van Soest, 1994) by sequential extraction using the fiber-bag method (Ankom, 2004). All samples were scanned in the near infrared (400-2498 nm) using an NIRSystems model 6500 scanning monochromator (Foss NIRSystems, Silver Spring, MD, USA) equipped with silicon (400-1098 nm) and lead sulfide (100-2498 nm) detectors with data collected every 2 nm (1050 data points) at a nominal bandwidth of 10 nm. Samples were scanned using a rotating sample cup and a ceramic standard

was used for the background spectrum and spectra were collected as $\log(1/R)$ where R = reflectance. Each spectrum consisted of 64 coadded scans for the sample and background. Only data from 1100 to 2498 nm was used in calibration development. Calibrations were developed using a one-out cross-validation using partial least-squares regression (GRAMS PLSPlus V2.1 G, Galactic Industries, Salem, NH, USA) with a variety of data pretreatments. The final calibration was then used to predict all the samples and the predicted values used for all subsequent analysis. This method (Westerhaus *et al.*, 2004) provides the most efficient means to reduce the need for wet chemical analysis while providing accurate analytical values.

Design, data analysis. Given the limited number of chambers, and because pots do not represent valid replications, a randomized complete block design was utilized with runs over time as replications (blocks). Each chamber was assigned one of the four CO₂ treatments (i.e. all CO2 treatments occurred in all chambers). At the end of a given run, CO₂ treatments were reassigned to another chamber and the entire experiment was repeated. PAR, humidity and temperature were quantified prior to, and at the end of each run in order to determine within chamber and between chamber variability. Temperature, PAR, humidity and [CO₂] were also recorded every 15 min throughout a given run, and daily averages determined for each chamber. Temperature, PAR and humidity did not differ between chambers. Plants from a given elevation were grouped together, but groups were spaced so as to minimize mutual shading. Both individual plants (pots) within a group, as well as groups, were rotated every 2 weeks inside the chambers until 72 DAS to minimize border effects. The experiment was repeated four times, with each run

considered a replicate. All plant parameters were analyzed using a three-way analysis of variance with $[CO_2]$, plant age (DAS) and population as the classification variables (Statview, Cary, NC, USA). Treatment comparisons were made using a Fisher's protected least significant difference. Unless otherwise stated, significant differences for any measured parameter were determined at the P < 0.05 level.

Results

By 87 DAS, [CO₂] significantly increased leaf area, leaf weight, root weight, and vegetative biomass when averaged over all populations (Table 1). Rising [CO₂] also resulted in a significant increase in the amount of root relative to shoot biomass (R:S). Specific population effects independent of [CO₂] were also observed for leaf area, specific leaf area (SLA) and vegetative biomass, with [CO₂] by population interactions observed for leaf area, leaf weight and root: shoot ratio (Table 1). Overall, while all populations were [CO₂] sensitive, sensitivity decreased with increasing elevation. This is evident as well in the overall growth curves beginning at 25 DAS (Fig. 1). For the lowest elevation by 87 DAS, any [CO₂] above the 270 µmol mol⁻¹ preindustrial baseline resulted in a significant stimulation of total plant biomass. This same population also showed a doubling of reproductive biomass with increasing [CO₂] for this same period (Fig. 2). Concurrent with the increase in seed yield, recent increases in [CO₂] (270- $370 \, \mu \text{mol mol}^{-1}$) also reduced the time to reproductive maturity for this population by approximately 10 days.

Fuel load for fire is directly proportional to above-ground biomass. Significant effects of $[CO_2]$ on above-ground biomass were observed as early as 59 DAS, increasing an average of 75% with a 150 μ mol mol⁻¹ increase above 270 μ mol mol⁻¹ with no population by

Table 1 Averages and statistical *P*-values of the two-way analysis of variance for CO₂ concentration and population for vegetative characteristics at 87 days after sowing (DAS) for cheatgrass (*Bromus tectorum*)

	Averages							P-values			
Variable	270	320	370	420	E1	E2	E3	CO ₂ effect	E effect	$E \times CO_2$	
Leaf area (m ²)	0.83	1.02	1.32	1.24	1.39	0.95	0.98	*	**	**	
Leaf weight (g)	36.1	45.3	57.6	62.6	51.3	52.1	48.4	***	_	**	
Root weight (g)	18.6	28.4	35.0	45.0	31.7	32.8	31.4	***	_	(*)	
$SLA (m^2 kg^{-1})$	22.7	22.2	22.0	19.3	25.6	18.6	20.9	_	**	(*)	
Root:Shoot	0.53	0.64	0.66	0.73	0.65	0.62	0.65	***	_	***	
Vegetative biomass	55.6	77.6	94.3	111.4	90.0	84.9	79.8	***	*	_	

 $^{^{(*)}}P < 0.10$; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Unless otherwise specified, values are per plant. E1, E2 and E3 are populations collected at 1220, 1737 and 2171 m in northern Nevada, respectively. SLA, specific leaf area.

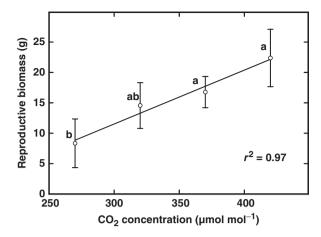


Fig. 2 Biomass (peduncle and seed, g per plant) of the lowest elevational cheatgrass population (1220 m) as a function of [CO₂]. Letters indicate Fisher's protected 1SD. Bars are \pm SE.

[CO₂] interactions (Fig. 3). However, by 87 DAS, a significant population by [CO2] effect was observed with a doubling of aboveground for the 1220 m population (+130%), compared with a 58% stimulation for the 2171 m population over the same [CO₂] range (Fig. 3). Overall, from 25 until 87 days after sowing (DAS), the populations used in this study showed an increase in aboveground biomass (vegetative and reproductive) of 1.5-2.7 g per plant for every 10 μmol mol⁻¹ increase above the 270 μmol mol⁻¹ preindustrial baseline.

In addition to the effect of rising [CO₂] on biomass, [CO₂] also affected qualitative parameters of cheatgrass. For the C:N data, [CO2], plant age and population were all significant as was [CO2] by age and population by age (Table 2). Overall, aboveground leaf tissue showed an increase in C:N ratio in response to rising [CO₂] only as the tissue aged, with the highest C:N ratio observed for the low elevation population. The increase in C:N is consistent with the total amount of ADF (i.e. undigestible cellulose and lignin) observed with increasing [CO₂], particularly for the low elevation population (Fig. 4).

Discussion

To better assess the impact of atmospheric [CO₂] on plant communities, it is critical to recognize interactions between CO₂ responsiveness and specific periodic disturbances such as fire. As summarized by Sage (1996), rising atmospheric [CO₂] would likely result in early stimulation of biomass production and a subsequent increase in the rate of fuel accumulation. As biomass production occurs more quickly, minimum fuel thresholds would be reached sooner between

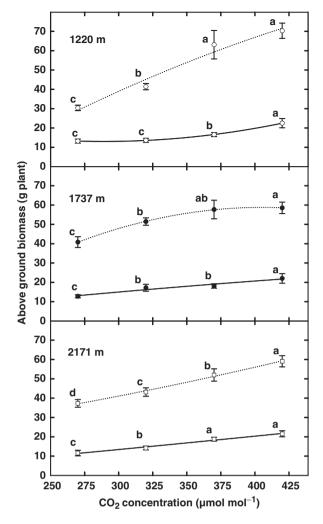


Fig. 3 Ground biomass at 59 and 87 days after sowing for three cheatgrass populations collected at different elevations as a function of [CO2]. Letters indicate Fisher's protected 1SD for each set of data connected by a line. Bars are \pm SE.

burns. Overall, more time would be spent proportionally above a minimum fuel threshold, leading to greater fire frequency if ignition probabilities remained unchanged. Greater biomass production by the end of the life-cycle would also increase total fuel available so that once a fire did occur; flame intensity, fire temperature and rate of spread would increase. Increases in intensity would, in turn, increase the probability that fire will damage the overstory or seedbank. This result, combined with greater fire frequency, would reduce the number of nonfire-adapted plants that reach reproductive maturity, potentially resulting in a decrease in species and structural diversity of the community.

Cheatgrass is an invasive species that is widely recognized as being fire adapted. Previous studies of fire-adapted annual grasses have indicated a high response to [CO₂] doubling (Smith et al., 1987, 2000;

Table 2 Changes in the ratio of carbon to nitrogen (C:N) as a function of atmospheric CO₂ concentration, by elevational population and by plant age

CO ₂	42 DAS			59 DAS			74 DAS			87 DAS		
	1221	1737	2174	1221	1737	2174	1221	1737	2174	1221	1737	2174
270	8.5	8.3	7.8	9.3	8.2	8.3	9.5	8.4	9.8	8.2	8.1	6.5
320	7.7	7.7	6.9	8.7	8.1	7.2	9.1	8.4	9.5	9.2	7.1	7.8
370	9.4	8.4	9.3	10.5	9.1	9.4	10.9	8.9	10.6	9.4	9.8	8.5
420	8.1	7.3	7.6	10.4	9.9	8.3	9.2	9.2	8.3	9.9	9.2	8.5

 $\begin{array}{lll} \text{CO}_2 & P = 0.0176^* \\ \text{Population} & P = 0.0538^* \\ \text{DAS} & P < 0.0001^{***} \\ \text{CO}_2 \times \text{DAS} & P = 0.0126^* \\ \text{Population} \times \text{CO}_2 & P = 0.9651 \\ \text{Population} \times \text{DAS} & P = 0.0152^* \\ \text{Population} \times \text{CO}_2 \times \text{DAS} & P = 0.2824 \\ \end{array}$

Elevations are in meters. Increased C:N is associated with a reduction in microbial decomposition.

DAS, days after sowing.

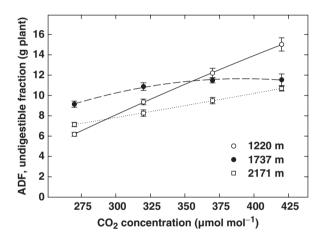


Fig. 4 The undigestible (ADF) portion of aboveground material (g per plant) as a function of increasing CO_2 . Significant increases in aboveground undigestible fractions of cheatgrass were observed for all populations with increasing $[CO_2]$ over the range 270– $420\,\mu\text{mol mol}^{-1}$. Bars are \pm SE.

Bazzaz 1990; Hunt *et al.*, 1991). The current experiment confirms this sensitivity to [CO₂], but also illustrates that cheatgrass may have potentially responded to recent increases in atmospheric [CO₂] during the later half of the 20th century. It is also interesting to note that cheatgrass may even respond significantly to short-term projections of 50 µmol mol⁻¹ above the current Mauna loa average; concentrations that are already present near urban areas (Ziska *et al.*, 2001). It could be argued that limitations of light, nutrients or water would negate the response of cheatgrass to atmospheric CO₂ *in situ*; however, fire increases light availability, temporarily enhances soil nutrient levels, and initially

reduces competition for water and nutrients (Blank *et al.*, 1994). Furthermore, *in situ* conditions following establishment suggest that at least once per decade, optimal water and nutrient conditions occur for supraoptimal cheatgrass growth (J. Young, unpublished data).

Overall, the current study indicates that even a small change in atmospheric [CO₂] could alter several key productivity parameters in cheatgrass that could affect fire disturbance. For example, by 59 DAS, [CO₂] had significantly increased the amount of aboveground biomass at current CO2 levels (relative to the 270 μmol mol⁻¹, preindustrial baseline) in all populations, suggesting an increase in the rate of fuel accumulation and a greater amount of time above a critical fuel threshold. Although the degree of carbon dioxide induced changes in final biomass appears population dependent, it is clear that rising [CO₂] may increase the total fuel availability of cheatgrass with subsequent changes in flame intensity and fire spread. Assuming that combustion probabilities are unchanged, this would suggest that recent changes in [CO₂] may have increased the fire frequency of cheatgrass during the 20th century. From an ecological perspective, CO₂-induced changes in fire frequency, combined with changes in reproductive output (at least for the 1220 m population), may have contributed to the establishment and success of cheatgrass in the western US by increasing seed production and eliminating competition from existing native perennial shrubs.

In addition to altering productivity parameters, [CO₂] may also alter qualitative aspects of cheatgrass that could affect fuel load. For example, cheatgrass is a major forage of herbivores, including insects, rabbits,

horses, mule deer and livestock (e.g. Murray & Klemmedson, 1968; Bishop et al., 2001). Cheatgrass matures quickly, with lower elevational (drier) ecotypes tending to mature earlier (Rice et al., 1992), but in any case, the time of maximum forage quality is usually much less than native perennial grasses. Increasing [CO₂] appears to increase the amount of undigestible aboveground material. Although in situ studies of herbivory are needed, CO2-induced changes in digestibility, reduced time till reproductive maturity and greater root: shoot ratios may, potentially, reduce herbivory rates or allow greater regrowth once herbivory occurs depending on population. Another qualitative aspect of [CO₂] may be related to decomposition. In the current study, increases in C:N ratio with increasing [CO₂] indicate a potential reduction in bacterial decomposition (Lambers, 1993). If bacterial decomposition occurs more slowly in response to rising [CO₂], then more rapid fuel accumulation is likely.

Fire damage in plant communities is directly impacted by fuel load which, in turn, is dependent on aboveground biomass. Fuel load directly alters fire occurrence (time spent above a critical threshold for burn), its rate of spread (less bare soil) and its intensity (increased ability to burn even with high humidity or cool nights). The current study suggests that rising [CO₂] may have already significantly affected the growth and establishment of cheatgrass during the 20th century, with subsequent effects on fuel load. These [CO₂]-induced changes in fuel load may have occurred directly through increased productivity, or indirectly through removal of standing biomass (e.g. herbivory, decomposition). Overall, the recent and near-term increases in atmospheric [CO2] suggest a probable link between the CO₂ responsiveness of this invasive grass, and fire disturbance.

At present, however, it is difficult to quantify the extent to which cheatgrass productivity has already been altered in situ. Although field evaluations are needed to address such issues, methodological considerations prevent exposure of plants to subambient CO₂ under realistic conditions (see Mayeux et al., 1993). Additional work on land-use change, particularly urbanization, is also needed to quantify cheatgrass establishment and growth. This does not, of course, lessen the importance of understanding how recent increases in atmospheric [CO2] may have impacted cheatgrass productivity and how such changes in turn, alter fire disturbance.

The current study, while limited to growth chamber conditions, does provide the first evaluation between recent [CO₂] increases, cheatgrass biology and potential changes in fire frequency. However, additional evaluations are needed, particularly those that examine the impact of rising [CO₂] on other qualitative parameters that affect combustibility. Such evaluations are necessary to further address the potential environmental consequences posed by cheatgrass and other invasive grasses as atmospheric [CO₂] continues to increase.

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